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RESEARCH ARTICLE

Enlarged lantern size in similar-sized, sympatric, sibling species of Strongylocentrotid sea urchins: from phenotypic accommodation to functional adaptation for durophagy

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Abstract *Strongylocentrotus droebachiensis* is a well known omnivorous sea urchin with an unrivalled capacity to destroy North Atlantic kelp forests. *S. pallidus* is a lesser known, morphologically similar, and closely related species with no record of destructive grazing, despite its larger lantern size. I quantify the lantern size of both species using bivariate allometric analysis, and test the hypothesis that enlarged lantern size facilitates durophagy, the consumption of hard prey, by measuring the feeding capacity of urchins with different lantern sizes when offered a hard-shelled prey, the blue mussel, *Mytilus edulis*. The results suggest that *S. droebachiensis* has a limited capacity for durophagous feeding irrespective of lantern size, whereas in *S. pallidus* the ability to exploit hard shelled prey is positively related to lantern size. This is apparently the first evidence of a relationship between trophic morphology and diet in regular sea urchins. The hypothesis of systematic latitudinal variation in the lantern size of *S. pallidus* is reappraised and rejected. *S. droebachiensis* had larger gonads than *S. pallidus* in field samples, confirming that its small lantern is not impeding nutrient acquisition in shallow habitats.

Introduction

The congeneric sea urchins *Strongylocentrotus droebachiensis* and *S. pallidus* are ideal candidates for the study of how divergent evolution leads to minor adaptations with major ecological consequences. These closely related (Biermann et al. 2003), morphologically similar species (Vasseur 1951; Swan 1962; Jensen 1974; Gagnon and Gilkinson 1994) are the only representatives of the sea urchin genus *Strongylocentrotus* in the Atlantic Ocean. Yet their ecological impact is remarkably different. *S. droebachiensis* is notorious for its unrivalled ability to reduce primary productivity and coastal biodiversity through widespread overgrazing of kelp forests (Hagen 1983; Chapman and Johnson 1990; Scheibling and Hatcher 2007), whereas *S. pallidus*, although sympatric throughout most of the Arctic-boreal distributional range, is more reclusive and occurs further to the north, at much lower densities, or in deeper habitats (Jensen 1974; Gilkinson et al. 1988; Bluhm et al. 1998).

S. droebachiensis and *S. pallidus* are the most recently diverged species pair in the genus *Strongylocentrotus*. They diverged 2.1–3.1 million years ago (Lee 2003; Dayal et al. 2004), but the separation from their closest relative *S. purpuratus* occurred during an earlier burst of Strongylocentrotid speciation in the North Pacific (Palumbi and Kessing 1991; Biermann et al. 2003), coinciding with the initial opening of the Bering Strait about 5 million years ago (Marincovich and Gladenkov 1999). They, or their common ancestor, subsequently invaded the North Atlantic as part of a major influx of species referred to as the trans-Arctic interchange (Vermeij 1991). It is noteworthy, as a preamble to the current ecological situation, that the evolution of Strongylocentrotid sea urchins in the North Pacific paralleled the evolution of their principal food source, the large brown algae known as kelp (Estes and Steinberg 1988), which also invaded the North Atlantic during the trans-Arctic interchange (Vermeij 1992).

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The ecological relationship between kelp and the Strongylocentrotid sea urchins ranges from kelp-dominated coexistence, to overgrazing followed by perpetuation of kelp-less, urchin-dominated barren grounds where the urchins persist relatively unimpeded under severe self-inflicted food limitation (Harrold and Pearse 1987). Resource acquisition under this extreme range of food availability is facilitated by the functional flexibility of the urchins' unique feeding apparatus, the Aristotle's lantern. This versatile and structurally complex organ is adapted for a general, omnivorous diet including soft sediments, hard calcified surfaces, and a wide array of plant and animal prey (De Ridder and Lawrence 1982).

The hypothesis that overall feeding capacity is directly related to, and limited by, lantern size is widely inferred (Lawrence 1987), as there is little evidence of structural or functional specialization of the lantern beyond "… an evolutionary progression towards a stronger, more efficient feeding apparatus for a general diet" (Lawrence 1975, p. 240). Lawrence et al. (1995) accordingly suggested that *S. franciscanus*, the largest member of the genus, owes its great size to an unusually large lantern, which presumably facilitates higher feeding rates and greater organic production. In *S. pallidus*, however, enlarged lantern size relative to *S. droebachiensis* (Vasseur 1951), is still a puzzling phenomenon (Gagnon and Gilkinson 1994), evidently not associated with larger maximum size (Jensen 1974), differences in growth rate (Vader et al. 1986), or greater organic production (Bluhm et al. 1998).

Some species, including *S. purpuratus*, respond to food limitation by enlarging lantern size through plastic allocation of resources from body growth to lantern growth (Ebert 1980, 1996; Russell 1987; Edwards and Ebert 1991), but the lantern size of *S. droebachiensis* is so similar in different sampling locations (c.f. Vasseur 1952; Russell 2001), that the notion of phenotypic plasticity has been rejected by Lawrence et al. (1998). The only test of the associated hypothesis, that environmentally induced enlarged lantern size facilitates acquisition of scarce food, is provided by Black et al. (1984), who found a positive correlation between enlarged lantern size and feeding capacity in the Australian urchin *Echinometra mathaei*. The results were not unequivocal, however, as urchins with smaller lanterns actually consumed 7.2 times more of the sea lettuce *Ulva lactuca*, and 2.8 times more of the kelp *Ecklonia radiata*, arguably the two best food items offered in their laboratory experiment (Black et al. 1984, Table IX), while urchins with larger lanterns consumed 2.9 times more of the calcified red algae *Metagonolithium* sp. A reinterpretation of these results is consistent with the hypothesis that urchins with small lanterns are superior consumers of high quality soft food, and conversely that enlarged lantern size facilitates durophagy, the consumption of hard prey.

In this study, I test the hypothesis that enlarged lantern size is a functional adaptation for durophagy by measuring the feeding capacity of urchins with different lantern sizes when offered a hard-shelled prey, the blue mussel, *Mytilus edulis*. Using bivariate allometric analysis (Warton et al. 2006), I quantify and compare the relative lantern sizes of *S. droebachiensis* and *S. pallidus* from Bodø, Northern Norway, to address the hypothesis of systematic latitudinal variation in the lantern size of *S. pallidus* (Vasseur 1952). I also examine the relationship between gonad size and lantern size in field populations in light of the urchins' durophagous feeding capacity. Finally, I reassess published data for lantern size variation in *S. purpuratus* and *S. franciscanus* and give a tentative interpretation of the role of lantern size in the speciation of *S. droebachiencis* and *S. pallidus*.

Materials and methods

Allometric analysis

Sampling

Morphometric data for the allometric analysis were obtained by dissecting 80 individuals of *S. droebachiensis* and 79 individuals of *S. pallidus* from two sampling locations in Bodø, northern Norway. The first sample was obtained from a tidal channel named Godøystraumen in February 2006 (67° 14′ 20″ N, 14° 43′ E; c.f. Hagen 1987), prior to the annual spawning season (Vasseur 1952; Falk-Pettersen and Lønning 1983), and the second sample was obtained 6 months later, in August, in Mørkvedbukta (67° 14′ 30″ N, 14° 34′ E), a small exposed bay next to the Marine Research Station of Bodø University College. Both samples were collected by SCUBA diving in overgrazed areas surrounded by scattered

Table 1 Estimates of measurement error in demipyramid length, test diameter and wet body mass of *Strongylocentrotus pallidus*, and *S. droebachiensis*, from Bodø, Norway

Variable	N	n_i	δ	s^2
Ln(Demipyramid Length)	159	3	0.00045	0.01575
Ln(Test Diameter)	159			0.01832
Initial error estimate	8	5	0.00058	
Second error estimate	60	5	0.00031	
Ln(Wet Body Mass)	159			0.16608
Initial error estimate	8	5	0.00176	
Second error estimate	60	5	0.00004	

N number of individuals; n_i number of repeat measurements; δ measurement error; s^2 sample variance

patches of intact kelp. There was no significant effect of location in preliminary allometric analyses of relative lantern size (SMA, $P > 0.05$; c.f. Warton et al. 2006), and data from the two locations were pooled in subsequent analyses.

All measurements of mass were recorded with an accuracy of 0.01 g using laboratory scales, and all measurements of length were recorded with an accuracy of 0.01 mm using electronic calipers. Prior to dissection

Table 2 Effect of measurement error on allometric analysis of the relationship between test diameter (X) and demipyramid length (Y) of *Strongylocentrotus pallidus*, and *S. droebachiensis*, from Bodø, Norway

Group	N	r^2	P	β	Ln(α)	α
S. droebachiensis	80	0.807	0.000	0.9714 (0.8801, 1.0723)	−1.495 (−1.869, −1.121)	0.2242
S. pallidus	79	0.627	0.000	0.9918 (0.8638, 1.1389)	−1.422 (−1.944, −0.944)	0.2412
Isometry						
S. droebachiensis			0.561	1		
S. pallidus			0.907	1		
Common slope			0.810	0.9783 (0.9031, 1.0598)		
Common elevation			0.000			
S. droebachiensis					−1.522	0.2183
S. pallidus					−1.371	0.2539
Analysis including estimates of measurement error: $\delta_{\ln(\text{Test Diameter})} = 0.00576$, $\delta_{\ln(\text{Demipyramid Length})} = 0.00045$						
S. droebachiensis	80	0.852	0.000	0.9740 (0.8932, 1.0621)	−1.505 (−1.834, −1.176)	0.2220
S. pallidus	79	0.685	0.000	0.9972 (0.8782, 1.1323)	−1.443 (−1.924, −0.961)	0.2362
Isometry						
S. droebachiensis			0.547	1		
S. pallidus			0.965	1		
Common slope			0.793	0.9813 (0.9139, 1.0539)		
Common elevation			0.000			
S. droebachiensis					−1.534	0.2157
S. pallidus					−1.382	0.2511

95% confidence limits for slope and intercept in parentheses

N number of individuals; r^2 coefficient of determination; P probability value; β slope of SMA-line; Ln(α) intercept of SMA-line; α constant of allometric equation

Table 3 Durophagous feeding experiments with small and large sea urchins, *Strongylocentrotus pallidus* and *S. droebachiensis*, using the blue mussel, *Mytilus edulis*, as prey

Date, duration and number of replicate urchins

Date	Duration (days)	*M. edulis* Size (mm)	*S. droebachiensis* Small	*S. droebachiensis* Large	*S. pallidus* Small	*S. pallidus* Large	Sum
Dec. 17 2005	2.7	10 ± 2.5	3	3			6
		20 ± 2.5	3	3			6
		30 ± 2.5	3	3			6
Dec. 30 2005	3.7	10 ± 2.5	6	6			12
		20 ± 2.5	6	6			12
		30 ± 2.5	6	6			12
Jan. 13 2006	3.7	10 ± 2.5			6	6	12
		20 ± 2.5			6	6	12
		30 ± 2.5			6	6	12
Feb. 24 2006	3.7	10 ± 2.5	6	6	6	6	24
		20 ± 2.5	6	6	6	6	24
		30 ± 2.5	6	6	6	6	24
Jun. 15 2006	3.7	25 ± 2.5	3	3	3	3	12
		35 ± 2.5	3	3	3	3	12
Total			51	51	42	42	186

Table 4 Allometric analysis of the relationship between urchin size and Aristotle's lantern size of *Strongylocentrotus pallidus* and *S. droebachiensis*, from Bodø, Norway

Group	*N*	r^2	*P*	β	Ln(α)	α	α-ratio
X: Test diameter							
Y: Wet lantern mass			0.393	2.650 (2.452, 2.865)			
S. droebachiensis	80	0.829	0.000		−9.816	0.000055	0.60
S. pallidus	79	0.610			−9.299	0.000092	1.68
Y: Lantern dry mass			0.211	2.565 (2.386, 2.760)			
S. droebachiensis	80	0.852	0.000		−10.032	0.000044	0.57
S. pallidus	79	0.665			−9.469	0.000077	1.76
Y: Lantern calcite			0.216	2.689 (2.496, 2.899)			
S. droebachiensis	80	0.839	0.000		−10.646	0.000024	0.55
S. pallidus	79	0.662			−10.057	0.000043	1.80
Y: Lantern calcite-free dry mass			0.336	2.291 (2.046, 2.566)			
S. droebachiensis	80	0.581	0.000		−11.076	0.000015	0.64
S. pallidus	79	0.368			−10.635	0.000024	1.55
X: Wet body mass							
Y: Wet lantern mass			0.269	0.911 (0.846, 0.981)			
S. droebachiensis	80	0.850	0.000		−3.068	0.047	0.56
S. pallidus	76	0.640			−2.490	0.083	1.78
Y: Lantern dry mass			0.123	0.880 (0.821, 0.944)			
S. droebachiensis	80	0.870			−3.493	0.030	0.54
S. pallidus	76	0.685			−2.873	0.057	1.86
Y: Lantern calcite			0.148	0.923 (0.859, 0.992)			
S. droebachiensis	80	0.855	0.000		−3.792	0.023	0.52
S. pallidus	76	0.682			−3.143	0.043	1.91
Y: Lantern calcite-free dry mass			0.241	0.789 (0.707, 0.882)			
S. droebachiensis	80	0.617	0.000		−5.250	0.005	0.61
S. pallidus	76	0.393			−4.759	0.009	1.63
X: Lantern dry mass							
Y: Lantern calcite-free dry mass			0.903	0.885 (0.801, 0.979)			
S. droebachiensis	80	0.637	0.08		−2.118	0.120	1.06
S. pallidus	79	0.562			−2.177	0.113	0.94

The slope and elevation of the logarithmic allometric equation, $\ln(Y) = \ln(\alpha) + \beta\ln(X)$, were determined using standardized major axis (SMA) estimation. 95% confidence limits for slope in parentheses

N number of individuals; r^2 coefficient of determination; *P* probability value; β slope of SMA-line; Ln(α) intercept of SMA-line; α constant of allometric equation; α-ratio: multiplicative difference in lantern size when there is a common slope and significant shift in elevation between the two species

the wet mass, test diameter, and test height were determined. Following dissection, measurements were obtained of gonad wet mass, lantern wet mass, lantern height, and lantern diameter. Lantern dry mass was determined after ≈24 h drying in a 105°C oven. Organic matter was removed from the lantern by ≈48 h submersion in a 3 Mol solution of NaOH, and the combined calcite mass of the lantern ossicles was determined after rinsing in fresh water and air drying. Lantern calcite free dry mass was estimated as the difference between combined calcite mass of the lantern ossicles and lantern dry mass. Demipyramid length was determined by measuring the distance between the tip and the epiphysis junction for three demipyramids from each lantern (Ebert 1980).

Allometric equation

The relationship between body size and lantern size was analysed using the general allometric equation (Ebert 1988; Reiss 1991):

$$Y = \alpha X^{\beta}. \quad (1)$$

After logarithmic transformation the relationship becomes linear:

$$\ln(Y) = \ln(\alpha) + \beta \ln(X). \quad (2)$$

Slopes and elevations of the linear equation (2) were estimated and compared using standardised major axis (SMA) estimation, the preferred choice in current bivariate line-fitting methods for allometry (Falster et al. 2006; Warton et al. 2006). Unlike ordinary least squares (OLS) regression, the SMA relation is symmetrical (Ricker 1984), i.e. insensitive to the choice of body size or lantern size as *X* or *Y*, but the method requires a posteriori assessment of the magnitude of measurement error in both variables and its overall effect on the outcome of the analysis (Warton et al. 2006).

Measurement error

Estimates of measurement error were calculated according to Warton et al. (2006, p. 283, Eqs. 31, 34, Example 4). For demipyramid length measurement error was estimated from repeated measurements of three demipyramids from the lantern of each of the 159 urchins in the entire sample. The estimated value, 0.00045, is small compared to the value of the sample variance, $S^2_{\ln(\text{Demipyramid Length})}$ = 0.01575 (Table 1).

Measurement errors for test diameter and total body mass were estimated independently: first from an initial sample of eight urchins that were each measured five times; then 60 additional urchins were measured in the same way, and combined with the first sample to provide data for a second estimate of measurement error. The initial estimates of measurement error are small compared to the values of the sample variances, and the second estimates were even smaller (Table 1).

The effect of accounting for measurement error was slight and had no effect on tests for isometry, common slope, or common elevation of the SMA lines relating demipyramid length and test diameter of the two urchin species (Table 2). Estimates of slope and elevation differed slightly when using the largest estimate of measurement error for test diameter, but the differences were almost indistinguishable when SMA curves were plotted. In conclusion, measurement error was small compared to sample variance, had negligible effect on estimates of slope and elevation, had no qualitative effect on statistical analyses of allometric relationships, and was, therefore, not given further consideration in the interpretation of the relative lantern sizes of *S. droebachiensis* and *S. pallidus*.

Feeding experiments

The durophagous feeding capacity of *S. pallidus* and *S. droebachiensis* was estimated in a series of five independently executed experiments involving a total of 186 urchins (Table 3). At the start of each experiment each urchin was placed individually in a 25 cm diameter glass bowl fitted with a perforated stainless steel collar and a separate supply of running seawater (≈7°C). Each bowl contained 25 mussels, *Mytilus edulis*, of similar size from one of several non-overlapping size ranges (Table 3). The shell length of all mussels was measured using electronic calipers. The average content of organic matter in the mussels was determined at the start of each experiment from samples of 25 individuals in each size range. The average mussel flesh dry mass of each sample was determined after ≈24 h drying in a 105°C oven.

The feeding capacity of each urchin was determined by subtracting the number of intact mussels at the termination of the experiment from the initial number, multiplying by the average mussel flesh dry mass of the appropriate size range, and expressed as the amount of mussel flesh dry mass consumed per day. Unsuccessfully attacked mussels were scored as intact when there was no damage to the

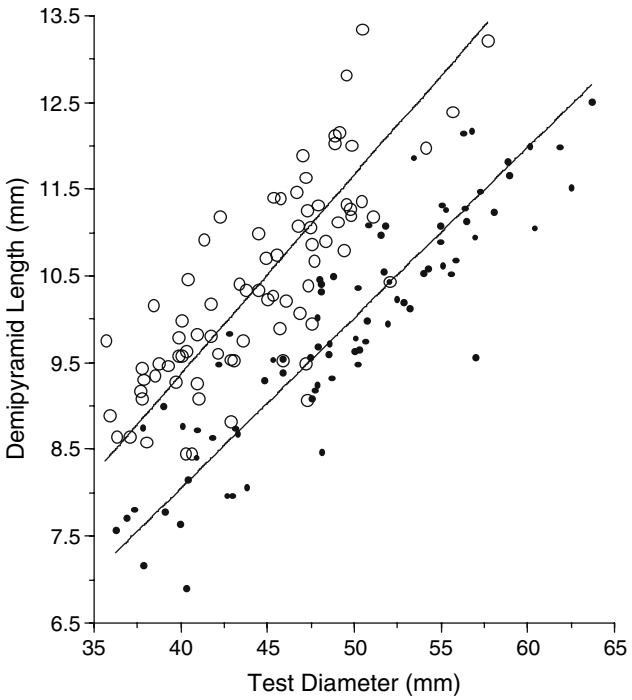

Fig. 1 Allometric relationship between test diameter and demipyramid length of *Strongylocentrotus pallidus* (*large open circles*), and *S. droebachiensis* (*small filled circles*), from Bodø, Norway

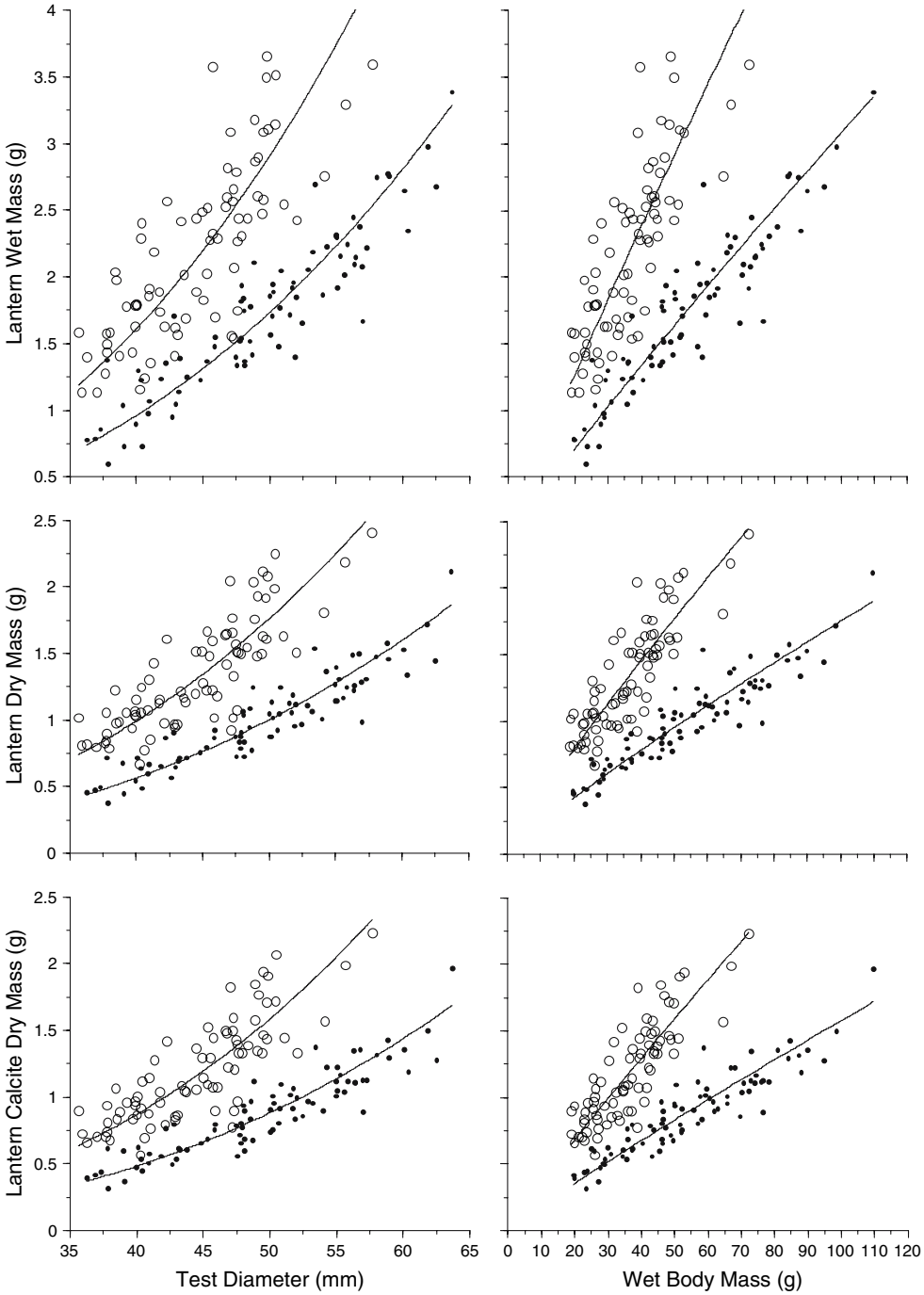

Fig. 2 Allometric relationships between urchin size (test diameter, wet body mass), and lantern size (wet mass, dry mass, calcite dry mass), of *Strongylocentrotus pallidus* (*large open circles*), and *S. droebachiensis* (*small filled circles*), from Bodø, Norway

flesh, and rare cases of partially consumed mussels were scored as 50% intact.

The lantern size of urchins in the feeding experiments was estimated using the allometric relations between test diameter and lantern dry mass established in Table 4. Only two size groups of urchins were used in the feeding experiments (test diameter: small ≈40 mm, large ≈50 mm, Fig. 4), but lantern sizes fell into three distinct groups: small (small *S. droebachiensis*), intermediate (large *S. droebachiensis* and small *S. pallidus*), and large (large *S. pallidus*) (Fig. 4).

Data from the feeding experiments were analysed using graphical methods, i.e. box plots, histograms and percentile comparison plots (Cleveland 1985), because parametric methods were rendered unsuitable by heteroscedasticity that could not be alleviated by data transformation (Sokal and Rohlf 1995).

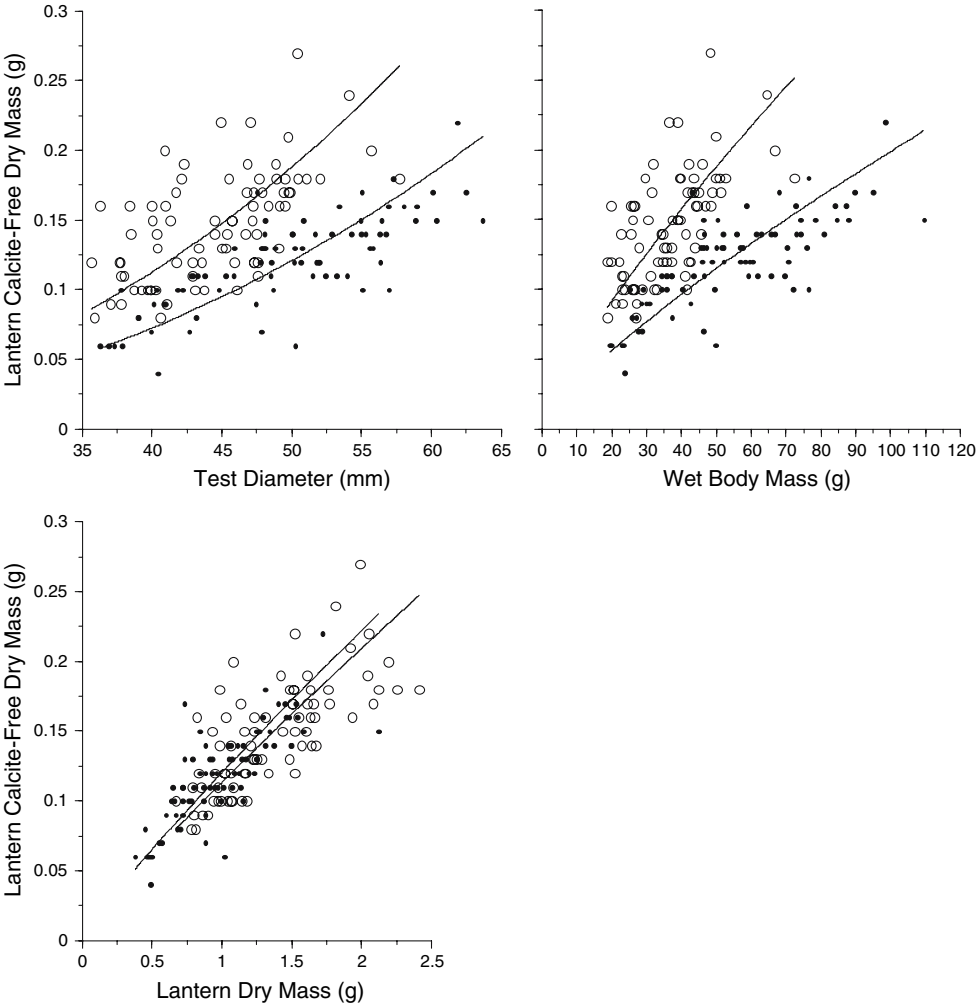

Fig. 3 Allometric relationships between urchin size (test diameter, wet body mass), lantern dry mass, and lantern calcite-free dry mass of *Strongylocentrotus pallidus* (*large open circles*), and *S. droebachiensis* (*small filled circles*), from Bodø, Norway

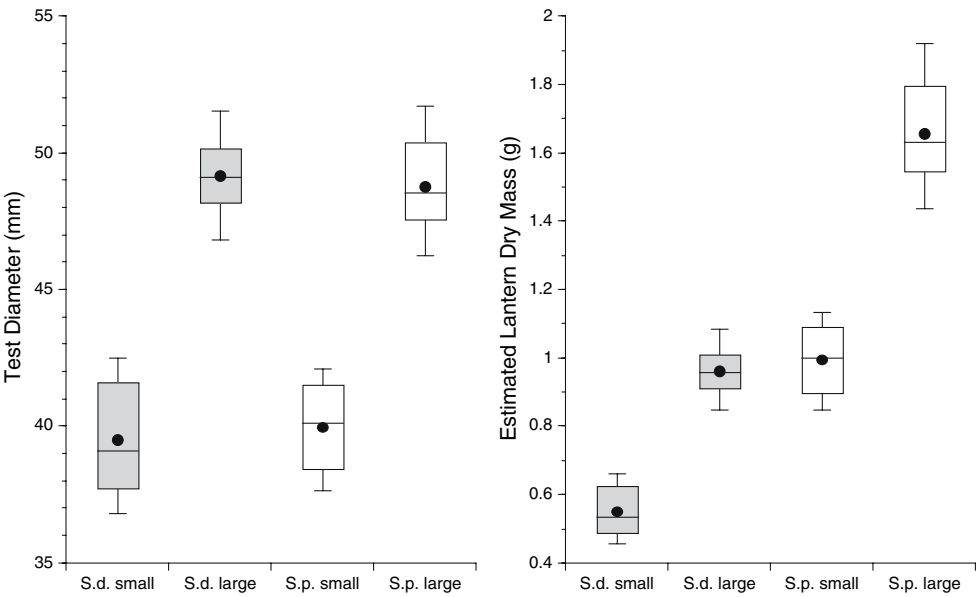

Fig. 4 Box-and-whisker plot comparing test diameter and estimated lantern size of the two size groups of *Strongylocentrotus droebachiensis* (*S.d. shaded boxes*, $N = 51$) and *S. pallidus* (*S.p. open boxes*, $N = 42$) used in the feeding experiments. The *top*, *bottom* and *line* through the middle of the *plotted boxes* represent the 75th, 25th, and 50th percentile (median) respectively. The whiskers extend from the ends of the box to the 10th and 90th percentiles, and the *circular symbol* is placed on the arithmetic mean

Results

Lantern Size

Allometry of test diameter and demipyramid length

The null hypothesis of isometry of test diameter and demipyramid length, H_0: $\beta = 1$, could not be rejected for either species ($P \geq 0.05$, Table 2). The test for common slope, H_0: $\beta_{S.\ droebachiensis} = \beta_{S.\ pallidus}$, although superfluous when the relationship is isometric, was also non-significant, and the common slope was estimated as $\beta = 0.9783$ ($P \geq 0.05$, Table 2). When there is a common slope, the next step in the allometric analysis is to test the null hypothesis of equal elevation, H_0: $\ln(\alpha_{S.\ droebachiensis}) = \ln(\alpha_{S.\ pallidus})$. A significant test result indicates that the lantern sizes of the two species differ by a fixed ratio $\neq 1$, e.g. an α-ratio for demipyramid length of 1.16 means that the average demipyramid length of *S. pallidus* is 1.16 times longer than that of a similar sized *S. droebachiensis* ($P < 0.001$, Table 2; Fig. 1).

Allometry of test diameter, body mass and lantern mass

All allometric analyses of the relationship between urchin size (test diameter, wet body mass) and lantern mass (wet mass, dry mass, calcite dry mass and calcite-free dry mass) gave similar results, indicating common slopes and unequal elevations with *S. pallidus* having a heavier Aristotle's lantern than *S. droebachiensis* (Table 4; Fig. 2). The size differential was <200% (i.e. α-ratio <2) for all components of lantern mass.

The estimated α-ratio of lantern calcite dry mass (1.91) is larger than the α-ratio of calcite-free dry mass (1.63), suggesting that *S. droebachiensis* may have proportionally more organic matter (i.e. muscle tissue, connective tissue and parts of the alimentary canal) in its lantern. However, the r^2-values for calcite free dry mass for both species were lower than for other components of lantern mass, and a direct analysis of the allometric relationship between lantern dry mass and lantern calcite-free dry mass (Table 4), indicated a common slope and no significant ($P > 0.05$) difference in elevation, i.e. similar amounts of organic matter in the lanterns of both species (Fig. 3).

The amount of variation explained by the allometric analyses is consistently larger for *S. droebachiensis* (higher r^2-values, Table 4), indicating that its lantern size was less variable than that of *S. pallidus*.

Effect of enlarged lantern size on durophagous feeding capacity

Urchins with large lanterns (large *S. pallidus*) consumed approximately four times more mussel flesh dry mass per day than urchins with small lanterns (small *S. droebachiensis*, Figs. 4, 5). However, urchins with similar, intermediate size lanterns also differed (Figs. 6, 7), with small *S. pallidus* consuming approximately three times more than large *S. droebachiensis* (Fig. 5). These results indicate that, in addition to and independent of lantern size, there is also a large inter-species effect on the durophagous feeding capacity of these closely related sea urchins.

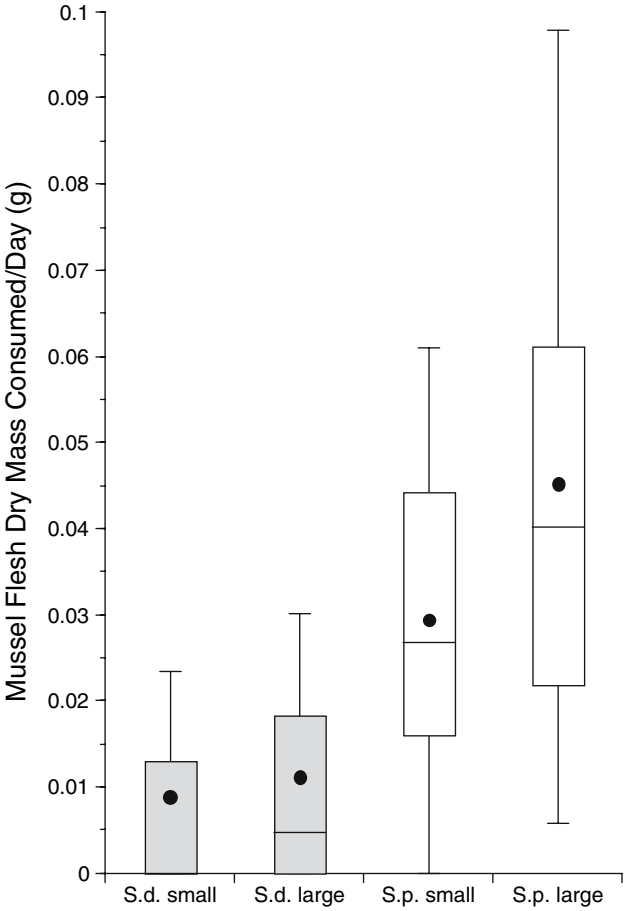

Fig. 5 Box-and-whisker plot comparing durophagous feeding capacity of the two size groups of *Strongylocentrotus droebachiensis* (*S.d. shaded boxes*) and *S. pallidus* (*S.p. open boxes*) used in the feeding experiments expressed as daily consumption of mussel dry mass. The *top*, *bottom*, and *line* through the middle of the *plotted boxes* represent the 75th, 25th and 50th percentile (median) respectively. The whiskers extend from the ends of the box to the 10th and 90th percentiles, and the *circular symbol* is placed on the arithmetic mean

The percentile plot contrasting small and large *S. pallidus* clearly shows that large urchins with large lanterns consume more mussel dry mass per day than small urchins with intermediate size lanterns (Fig. 7). In comparison, for *S. droebachiensis* there is only a modest effect of increased lantern size, most clearly indicated by a drop from 90% to <80% in the category of lowest consumption (<0.02 g mussel flesh dry mass per day), and a corresponding increase in the next category (Fig. 6). These results suggest that *S. droebachiensis* has a limited capacity for durophagy irrespective of lantern size, whereas in *S. pallidus* the ability to exploit hard shelled prey is positively related to lantern size.

Gonad size

Interestingly, *S. droebachiensis*, the species with the smallest lantern (Fig. 2), had the largest gonads in both field samples (Fig. 8). Gonad mass was variable, but increased rapidly for urchins >40 mm in test diameter. The variability was reflected in low coefficients of determination in the allometric analyses relating test diameter and lantern mass to gonad mass ($r^2 \leq 0.55$, Table 5). It was not possible to fit common slopes for both species ($P < 0.001$), and a post hoc multiple comparison of slopes among groups indicated that the steepest slope, i.e. the largest gonads relative to test diameter, were found in *S. droebachiensis* in the February sample from Godøystraumen (Table 5).

Both species had the larger gonad size in the February sample from Godøystraumen according to the allometric analysis of lantern mass and gonad mass (Table 5; Fig. 8). For *S. droebachiensis* the gonad size in February was approximately 3.2 times larger than in August, and for *S. pallidus* approximately 1.7 times larger.

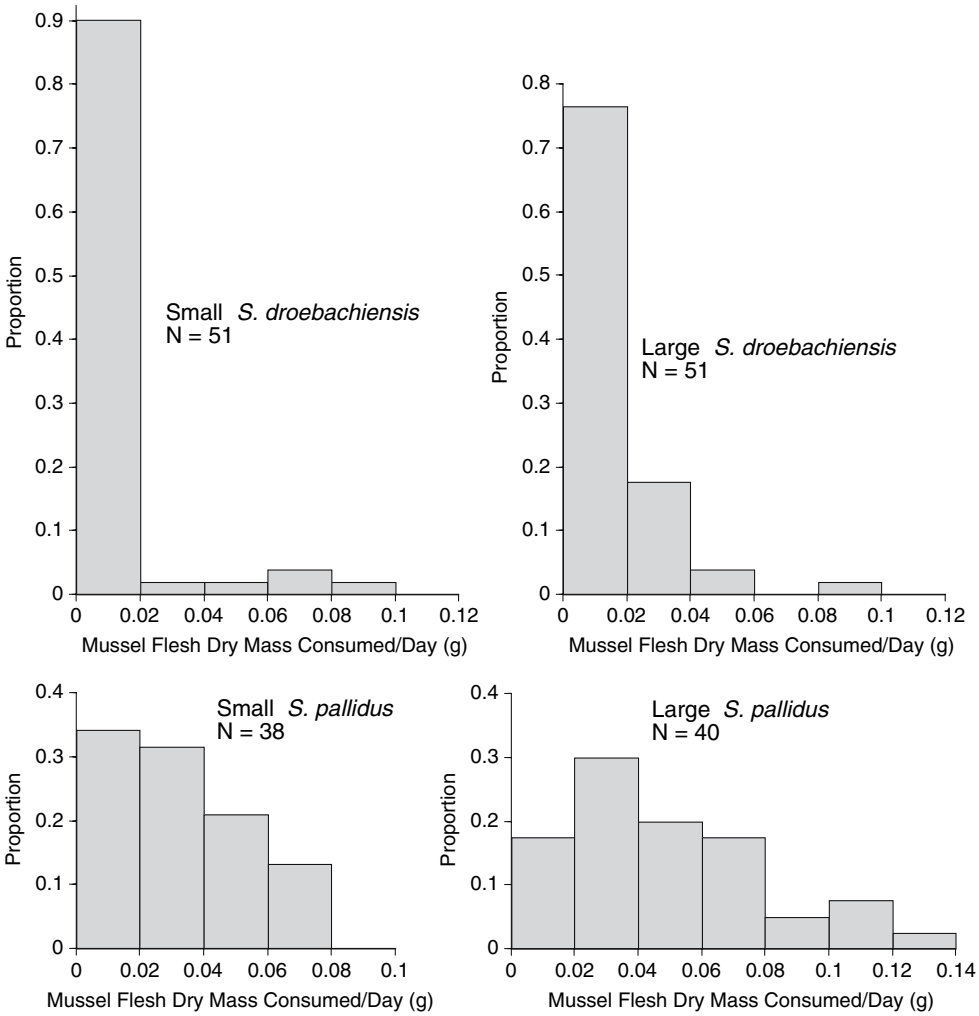

Fig. 6 Histograms comparing the durophagous feeding capacity of the two size groups of *Strongylocentrotus droebachiensis* and *S. pallidus*

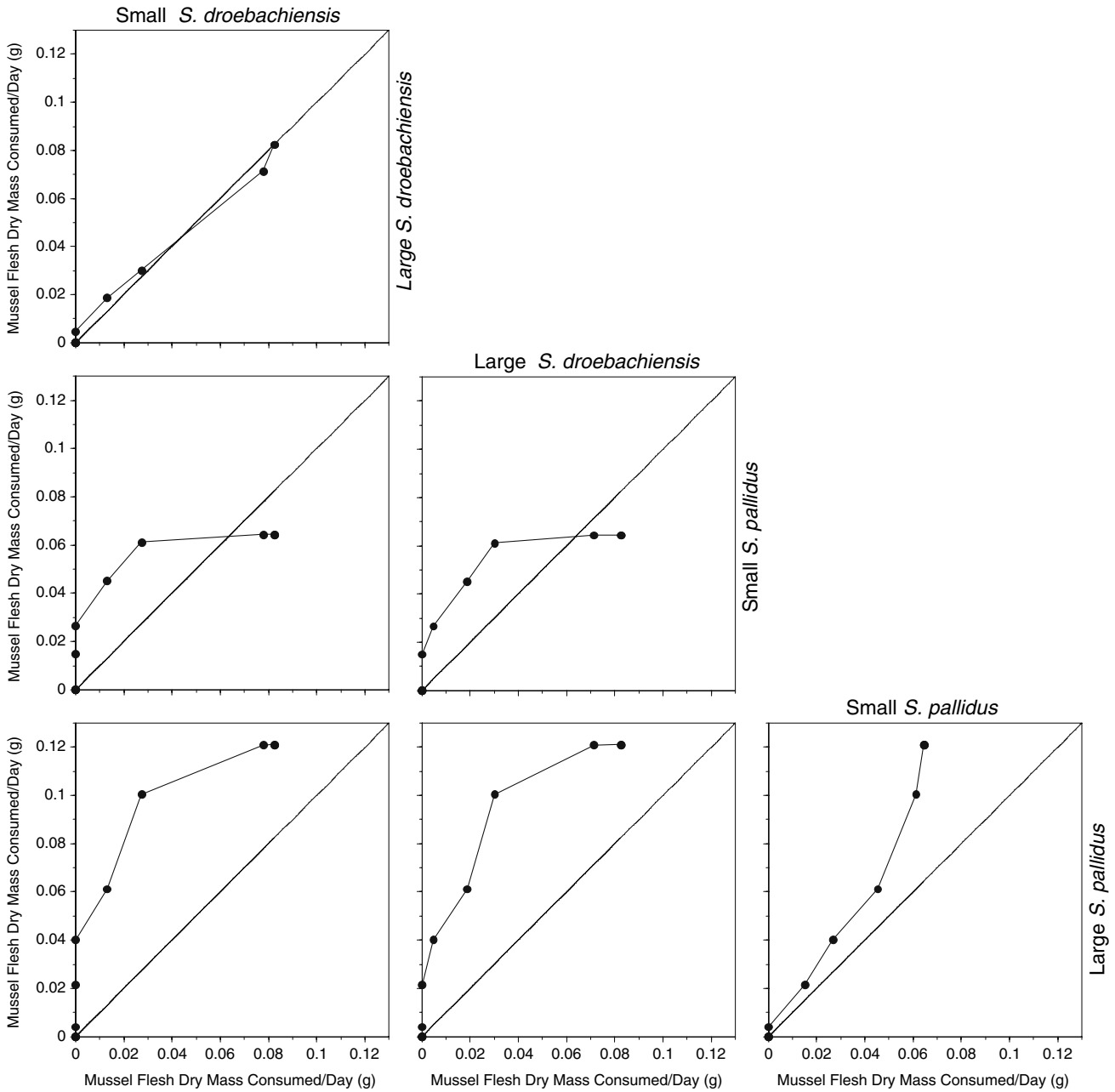

Fig. 7 Percentile plots comparing the durophagous feeding capacity of the two size groups of *Strongylocentrotus droebachiensis* and *S. pallidus*. The percentiles compared are 0.5, 2.5, 10, 25, 50, 75, 90, 97.5, 99.5 and 100

Discussion

Enlarged lantern size and durophagy

Strongylocentrotus pallidus from Bodø, Northern Norway differs from the closely related *S. droebachiensis* by having a larger Aristotle's lantern, and by having a much greater capacity for consuming hard shelled prey. These results are consistent with a hypothesis of enlarged lantern size being a functional specialization for durophagy, and is apparently the first evidence of a relationship between trophic morphology and diet in regular sea urchins. The hypothesis that enlarged lantern size is an adaptation for durophagy is also consistent with studies of sympatric sea urchins from different genera, where the species with the largest lantern occupies microhabitats with a scarcity of soft food (Contreras and Castilla 1987; Fernandez and Boudouresque 1997).

However, contrary to the assumption of a direct relationship between lantern size and feeding capacity in strongylocentrotid sea urchins (Lawrence et al. 1995), there was also a large inter-specific difference in feeding capacity

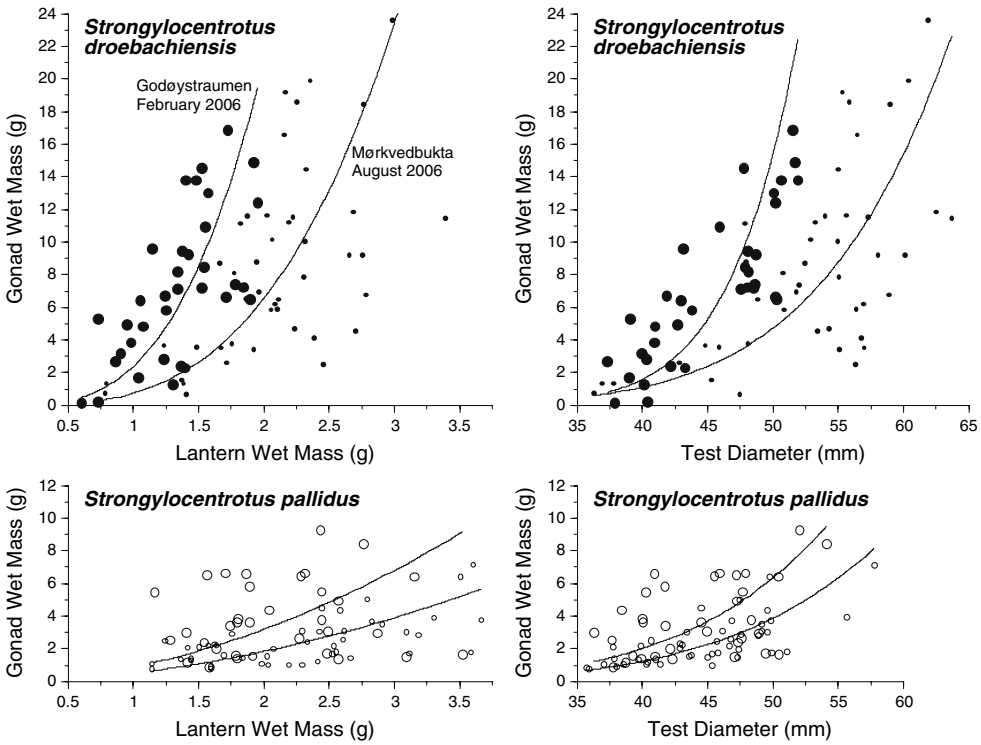

Fig. 8 Allometric relationships between size of the Aristotle's lantern, test diameter, and gonad size of *Strongylocentrotus pallidus* (*open circles*), and *S. droebachiensis* (*filled circles*), from two subtidal sampling locations in Bodø, Norway: Godøystraumen February 2006 (large symbols, *upper curve*) and Mørkvedbukta August 2006 (small symbols, *lower curve*)

Table 5 Allometric analysis of the relationship between test diameter, size of the Aristotle's lantern and gonad size of *Strongylocentrotus pallidus* and *S. droebachiensis*, from two subtidal sampling locations in Bodø, Norway

Group	*N*	r^2	*P*	β	Ln(α)	α	α-ratio
X: Test diameter							
Y: Gonad wet mass							
S. droebachiensis							
Common slope			0.006				
Godøystraumen February 2006	35	0.546	0.000	10.175 (8.034, 12.888)	−37.07	$<10^{-7}$	
Mørkvedbukta August 2006	45	0.533	0.000	6.486 (5.265, 7.991)	−23.82	$<10^{-7}$	
S. pallidus							
Common slope			0.138	5.156 (4.337, 6.137)			
Godøystraumen February 2006	34	0.166			−18.322		0.61
Mørkvedbukta August 2006	45	0.550			−18.813		1.63
X: Lantern wet mass							
Y: Gonad wet mass							
S. droebachiensis							
Common slope			0.199	3.143 (2.669, 3.694)			
Godøystraumen February 2006	35	0.514			0.870	2.387	3.22
Mørkvedbukta August 2006	45	0.514			−0.298	0.742	0.31
S. pallidus							
Common slope			0.128	1.860 (1.518, 2.279)			
Godøystraumen February 2006	34	0.011			−0.126	0.882	0.57
Mørkvedbukta August 2006	45	0.357			−0.682	0.506	1.74

The slope and elevation of the logarithmic allometric equation, $\ln(Y) = \ln(\alpha) + \beta\ln(X)$, were determined using standardized major axis (SMA) estimation. 95% confidence limits for slope in parentheses

N number of individuals; r^2 coefficient of determination; *P* probability value; β slope of SMA-line; Ln(α) intercept of SMA-line; α constant of allometric equation; α-ratio multiplicative difference in lantern size when there is a common slope and significant shift in elevation between the two samples

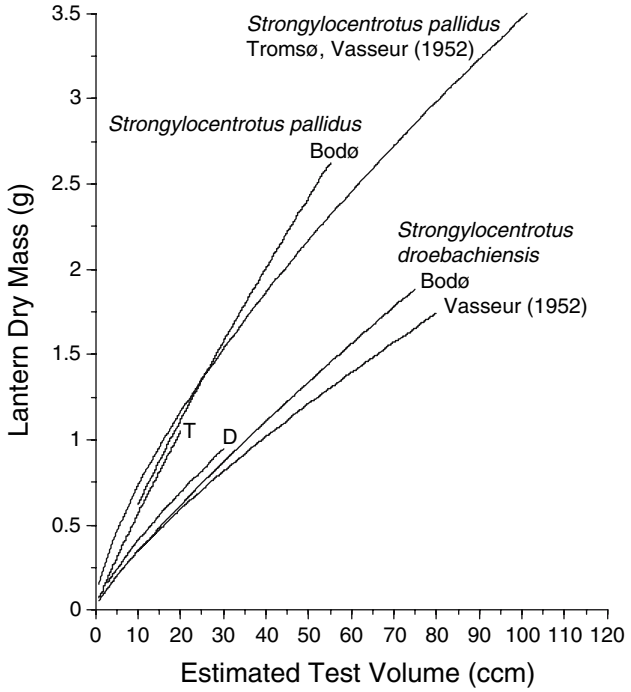

Fig. 9 Back-transformed SMA curves relating estimated test volume and dry mass of the Aristotle's lantern of *Strongylocentrotus pallidus* and *S. droebachiensis* from Bodø, in comparison with curves estimated from data in Vasseur (1952, Figs. 2, 3, 4). Separate curves are fitted for *S. pallidus* from Tromsø, Trondheim (*T*) and Drøbak (*D*), and a single curve is fitted for *S. droebachiensis* from the same sites. The length of the curves covers the range of data in each sample

between urchins with similar lantern size, i.e. large *S. droebachiensis* and small *S. pallidus*. The latter result indicates the existence of additional adaptations for durophagy in *S. pallidus*. Such adaptations would appear to be unrelated to the amount of muscle tissue in the lantern, as there was no significant difference in the amount of organic matter (calcite-free dry mass) in the lanterns of the two species, or to lantern morphology which is also similar (Jensen 1974), but may possibly be related to a diagnostic difference in the number of pore pairs (tube feet), which tend to be larger in *S. pallidus* (Vasseur 1952; Jensen 1974). The functional effect of more tube feet has yet to be investigated, but durophagy may conceivably be facilitated by additional tube feet providing a firmer grip on hard shelled prey to counterbalance the pressure of the working teeth of the lantern.

A superior ability to exploit hard shelled prey provides evidence of adaptive divergence, and may explain the current dominance of *S. pallidus* in northern areas and deep water habitats, where the scarcity of macroalgae might be a greater impediment for *S. droebachiensis*. Field experiments confirm that consumption of intact mussels by *S. droebachiensis* is restricted by their hard shells (Briscoe and Sebens 1988), making a diet of intact mussels inferior to a macroalgal diet despite the fact that mussel flesh alone is a readily consumed, high quality food source in laboratory trials (Thompson 1982, 1984; Meidel and Scheibling 1999).

Latitudinal variation in lantern size

The results of the present study are in general agreement with earlier observations of enlarged lantern size in *S. pallidus* (Vasseur 1951, Fig. 3; 1952, Fig. 2; Vader et al. 1986, Fig. 4), but do not support the notion of a geographic trend towards decreased lantern size in southern latitudes as suggested by Vasseur (1952). When comparing the relative lantern sizes of *S. pallidus* and *S. droebachiensis* he observed that the Aristotle's lantern of *S. pallidus* was approximately twice the size of *S. droebachiensis* in Tromsø, northern Norway, but close to that of *S. droebachiensis* in Drøbak, southern Norway (the type locality of *S. droebachiensis*), and of an intermediate size in Trondheim, central Norway, and interpreted his observations as the result of a general trend towards decreased lantern size in southern areas.

I scanned Vasseur's (1952) original figures and used an image analysis program (ImageJ) to obtain an approximate facsimile of his data. However, a general comparison of the alleged size differences is not possible because the SMA curves for *S. pallidus* from the three sites could not be fitted with a common slope ($P < 0.05$), i.e. the relative difference in lantern size as observed by Vasseur depends on the size of the urchins.

The size of *S. pallidus* in the samples from Trondheim and Drøbak was considerably smaller than in the sample from Tromsø, and lack of a common slope means that the curve relating body size and lantern size for *S. pallidus* from Trondheim, although initially below the curve from Tromsø will, if extrapolated intersect and exceed the curve from Tromsø for urchins beyond an estimated test volume of approximately 32 cm^3 (Fig. 9). Bodø is located south of Tromsø, yet the curve for *S. pallidus* from Bodø [fitted using Vasseur's formula for estimated test volume = (Diameter^2 × Height)/2] also intersects and exceeds the curve from Tromsø beyond an estimated test volume of approximately 25 cm^3 (Fig. 9).

Furthermore, Vasseur's (1952) suggestion that the lantern of *S. pallidus* in Tromsø is approximately twice the size of *S. droebachiensis* is, according to his own data, only valid for urchins with an estimated test volume of 15 cm^3. For smaller urchins the difference is >2, and for larger urchins the difference is <2. For urchins with an estimated test volume of 45 cm^3 the difference is 1.81, the same as the multiplicative size difference (α-ratio) between the two species in Bodø.

Finally, Vasseur (1952) also suggested that there was no geographic variation in the relative lantern size of *S. droebachiensis* from Tromsø, Trondheim and Drøbak. This suggestion is supported by the SMA analysis which

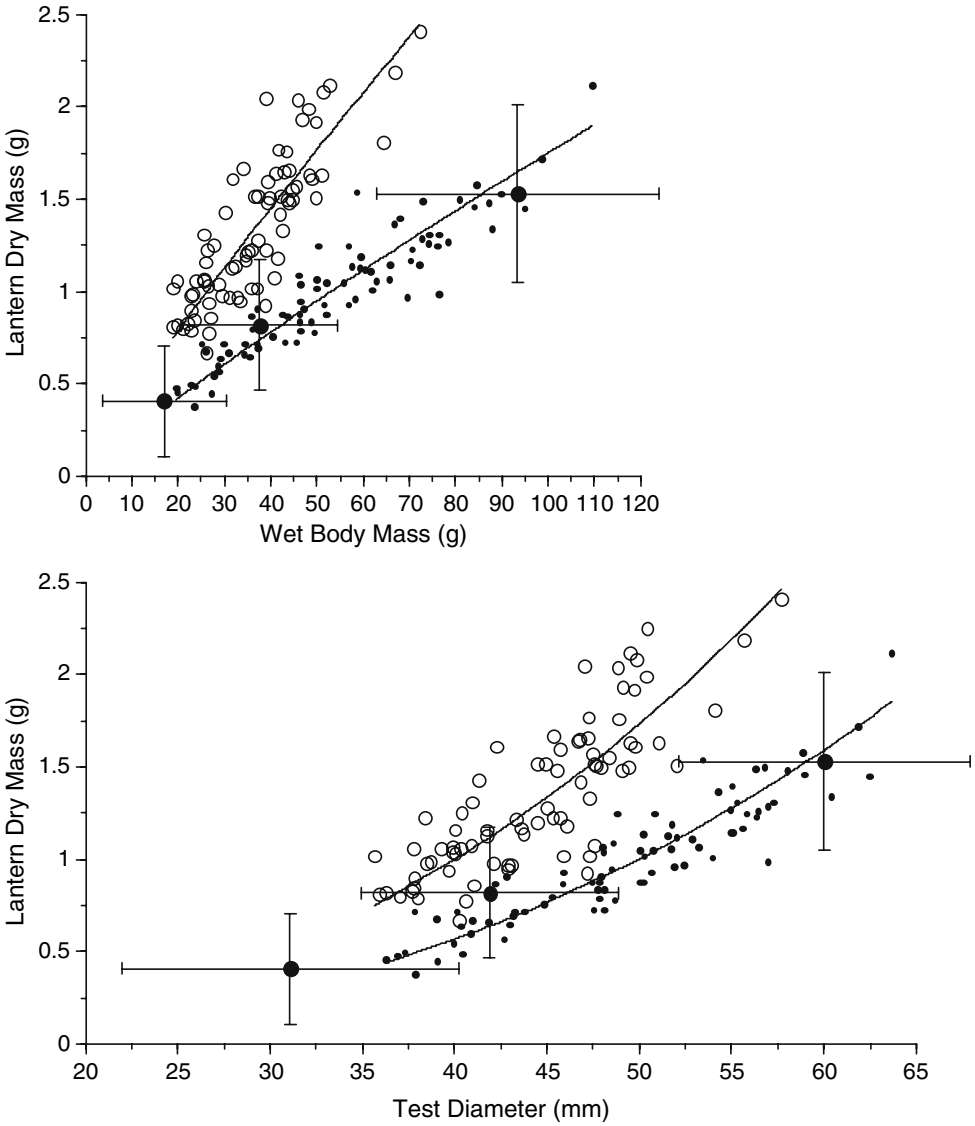

Fig. 10 Allometric relationships between urchin size and lantern dry mass of *Strongylocentrotus droebachiensis* (*small filled circles*), and *S. pallidus* (*large open circles*), from Bodø, Norway, in comparison with *S. droebachiensis* (*large filled circles* with standard deviation error bars) from Kamchatka, Russia (Lawrence et al. 1998)

detected no significant, site specific, difference in slope or elevation in his data for *S. droebachiensis*. It is also supported by Lawrence et al. (1998) who found no evidence of habitat related differences in the relative size of the Aristotle's lantern of *S. droebachiensis* from three locations in Kamchatka, Russia. Lawrence et al.'s (1998) observations from Kamchatka appear to fall within the size range of *S. droebachiensis* from Bodø (Fig. 10).

The lantern size of *S. droebachiensis* from Bodø is similar to Vasseur's (1952) pooled data (Fig. 9), and to Russell's (Russell et al. 1998, 2001) observations from Maine, USA (Fig. 11), for medium sized individuals, but the allometric curves diverge and urchins from Bodø appear to have larger lanterns at larger body size. However, these differences may at least in part be due to measurement error not being accounted for in the previous publications (c.f. Ebert 2004; Warton et al. 2006).

In conclusion, Vasseur's (1952) notion of systematic geographic variation in the relative lantern size of *S. pallidus* is only tenuously supported by his own sample of small urchins from Drøbak, and should probably be rejected, whereas his notion of similar lantern size of *S. droebachiensis* from different geographical areas is broadly consistent with the available evidence.

Gonad size and lantern size in field populations

S. pallidus had smaller gonads than *S. droebachiensis* at both sampling locations. Gonad size in sea urchins is a function of two factors: (1) the annual reproductive cycle and (2) food availability. *S. pallidus* spawns 2–3 months later than *S. droebachiensis* (Vasseur 1952; Falk-Pettersen and Lønning 1983), suggesting that its gonad size was still increasing in

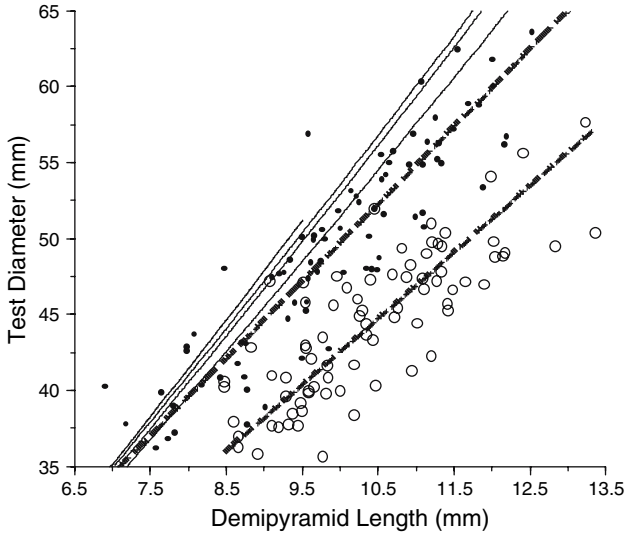

Fig. 11 Allometric relationships between demipyramid length and test diameter of *Strongylocentrotus droebachiensis* (*small filled circles*, *upper dashed line*), and *S. pallidus* (*large open circles*, *lower dashed line*), from Bodø, Norway, in comparison with *S. droebachiensis* (four thin lines) from Maine, USA (Russell et al. 1998; Russell 2001)

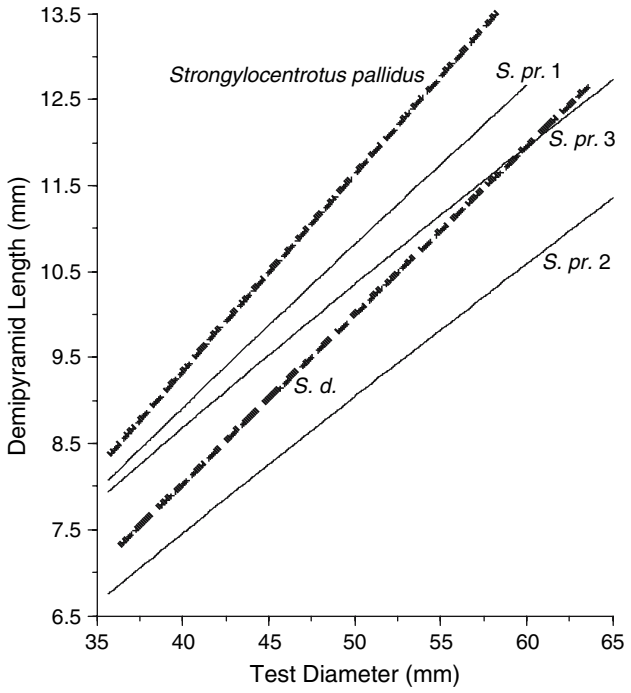

Fig. 12 Allometric relationship between test diameter and demipyramid length of the Aristotle's lantern of *Strongylocentrotus pallidus* (*upper dashed line*) and *S. droebachiensis* (*S. d.*, *lower dashed line*) from Bodø, Norway, in comparison with *S. purpuratus* from Oregon (*S. pr.* 1, 2, Ebert 1980) and California (*S. pr.* 3, Ebert 1996, Fig. 2)

the February sample, and still close to its annual post-spawning minimum in the August sample. The large discrepancy in gonad size between the two species would, nevertheless, suggest that *S. pallidus* was food limited, since

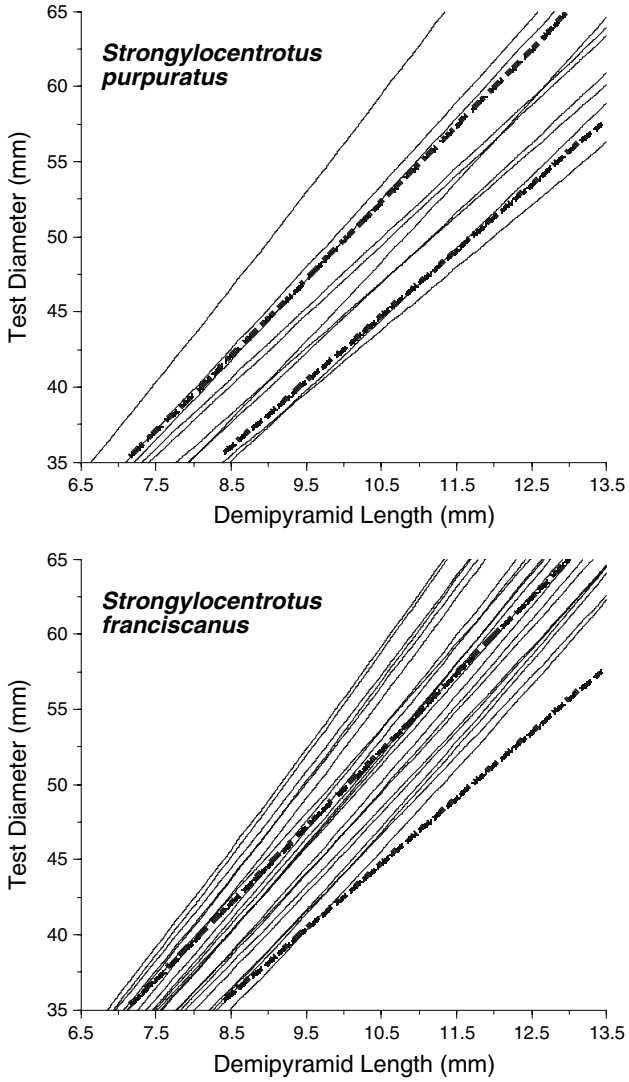

Fig. 13 Allometric relationship between demipyramid length of the Aristotle's lantern and test diameter of *Strongylocentrotus pallidus* (*lower dashed line*) and *S. droebachiensis* (*upper dashed line*) from Bodø, Norway, in comparison with *S. purpuratus* (Ebert 1980; Russell 1987) and *S. franciscanus* (Ebert and Russell 1992; Ebert et al. 1999; Rogers-Bennett et al. 2003) from the Northeast Pacific

its gonad size at both sampling sites was similar to the gonad size of *S. droebachiensis* in a food limited barren ground habitat (Hagen 1998). It is possible the food acquisition of *S. pallidus* in these shallow habitats was inhibited by competition from *S. droebachiensis* (Strathmann 1980), or by environmentally induced microhabitat preferences that may be more successful in deeper habitats.

Durophagy, the ability to efficiently exploit mollusks and other prey with hard exteriors, may be a beneficial trait in deep habitats where *S. pallidus* occurs in conspicuous density and maintains consistent gonad production (Gilkinson et al. 1988; Bluhm et al. 1998; Viktorovskaya and Zuenko 2005), while other Strongylocentrotids, including the deep water species *Allocentrotus fragilis* (Sumich and

McCauley 1973), are severely food limited or nonexistent in such habitats. An adaptation for durophagy may also explain relative success of *S. pallidus* in Arctic areas where severely restricted macroalgal vegetation makes seasonally abundant microalgal sediment an important food source (Viktorovskaya and Zuenko 2005), which presumably is more efficiently ingested by an urchin with enlarged lantern size (c.f. Black et al. 1984).

Lantern size of other Strongylocentrotids

The inter-specific variation in lantern size between *S. droebachiensis* and *S. pallidus* appears to encompass the same range of variation as the reported habitat related phenotypic variation in the lantern size of *S. purpuratus* (Figs. 12, 13) (Ebert 1980; Russell 1987). In contrast, the lantern size of *S. franciscanus* appears to be smaller than the lantern size of *S. pallidus* for urchins larger than 45 mm in test diameter (Fig. 13). This interpretation is contrary to the suggestion that *S. franciscanus* has a significantly larger lantern than other strongylocentrotid sea urchins (Lawrence et al. 1995), a discrepancy that may be a result of measurement error not being adequately accounted for in previous analyses (c.f. Ebert 2004).

Enlarged lantern size and speciation

The observed inter-specific differences in durophagy are consistent with a scenario of speciation facilitated by phenotypic accommodation followed by functional adaptation (West-Eberhard 2005; Pigliucci et al. 2006), where the range of phenotypic plasticity in lantern size still exhibited by *S. purpuratus* appears to have been canalized in opposite directions during the divergence of *S. droebachiensis* and *S. pallidus*. The latter species has successfully specialized in durophagy by retaining a large, variable lantern size, supported by a robust, polyporous skeleton, whereas *S. droebachiensis* has evolved a narrower, perhaps less costly, trophic morphology that favours opportunistic, invasive overexploitation of benthic vegetation at the expense of a reduced capacity for durophagy.

In conclusion, the results of this study are consistent with the hypothesis that enlarged lantern size constitutes a functional specialisation for durophagy, and point to the need for more information about the role of lantern size in the trophic ecology of sea urchins.

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Appendix

Table 6

Table 6 Literature survey af allometric relationships between lantern size and body size in Strongylocentrotid sea urchins

Species	Ln(α)	α	β	Units	Source	Comment
$D = \alpha J^{\beta}$						
Strongylocentrotus droebachiensis		3.34	1.20	mm	Russell (2001)	Intertidal and Sub 1
		3.21	1.23			Subtidal 2
		3.48	1.17	mm	Russell et al. (1998)	Tidepool 1
		3.38	1.20			Tidepools 2–7
Strongylocentrotus purpuratus		4.48	0.98	cm	Russell (1987)	VI1
		4.46	1.04			VI2
		4.76	0.98			VI3
		4.71	0.99			VI4
		4.17	1.00			SD1
		4.21	1.12			SD2
		5.07	1.08			PB1
		4.98	1.08			PB2
		4.5667	1.155	cm	Ebert (1980)	PZ and EG
		5.6197	1.155			Boulder Field

Table 6 continued

Species	Ln(α)	α	β	Units	Source	Comment
Strongylocentrotus franciscanus		4.4094	1.2437	cm	Ebert and Russell (1992)	San Nicolas Island
		3.31	1.15	mm	Rogers-Bennett et al. (2003)	Northern California
		4.926	1.175	cm	Ebert et al (1999; Table 5)	
		4.852	1.145			
		5.535	1.248			
		5.575	1.228			
		5.352	1.248			
		5.403	1.200			
		4.584	1.140			
		5.329	1.212			
		5.236	1.257			
		4.542	1.174			
		4.292	1.241			
		4.679	1.188			
		5.089	1.104			
		5.059	1.209			
		4.730	1.204			
		4.877	1.183			
		4.441	1.244			
		4.896	1.214			
		4.996	1.214			
		4.409	1.168			
$J = \alpha D^{\beta}$						
Strongylocentrotus purpuratus	−1.2322	(0.2917)	0.7871	cm	Ebert (1996)	Initial sample, Fig. 2
		0.2685	0.8658	cm	Ebert (1980)	PZ and EG
		0.2245	0.8658			Boulder Field
Strongylocentrotus franciscanus	−0.805	(0.4471)	0.796	mm	Morris and Campbell (1996)	Wild sample
	−0.613	(0.5417)	0.735			Starved
	−0.723	(0.4853)	0.760			*Zostera*
	−1.214	(0.2970)	0.866			*Nereocystis*

D test diameter; *J* demipyramid length; Ln(α) intercept, α allometric constant, β slope of allometric equation. α-values in parentheses are converted from ln(α)-values in the source publication

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